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Growth and survival of barnacles in presence of co-dominating solitary ascidians: growth ring analysis

Marina Varfolomeeva, Anna Artemieva, Natalia Shunatova, Eugeniy Yakovis *

Invertebrate Zoology Department, St.-Petersburg State University, Universitetskaya nab. 7/9, 199034, St.-Petersburg, Russia

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ABSTRACT

Marine and terrestrial communities are often hierarchically structured by one or more foundation species, which provide habitats for many other taxa. Interactions between coexisting habitat modifiers may have strong effects on patterns and processes in the dependent assemblage. Yet they are rarely studied, especially at a small scale.
Small epibenthic patches co-dominated by barnacles *Balanus crenatus* Brugiere and several species of solitary ascidians in the White Sea soft bottoms support many dependent species. Barnacles occupy bivalve shells, small stones and conspecifics. Ascidian clumps develop on barnacles and their empty shells. Previous observations suggest that at the patch scale ascidians may replace barnacles over several years likely because of the negative interactions between them. Barnacles have distinct annual growth rings on their shells, which we used to trace their growth and survival in the field. No difference between the patches with different dominants would evidence no pronounced negative effect of ascidians.
In the patches dominated by ascidians (A) or barnacles (B) collected at the same subtidal site in 2004 and 2005 we compared lengths of recent annual vertical growth increments and dead:live ratios of barnacles of the same age class according to the growth rings. Barnacles grew slower in A than in B, regardless of the biomass of conspecific neighbors. Dead:live ratios were higher in A for age classes 1+…2+ and 4+…9+. Estimated mortality risk between A and B increased with age of barnacles, from around 1:1 to 5.6 times greater in the 9+ age group. Because of the observed difference in growth and survival, the negative effect of adult ascidians on barnacles could not be excluded; alternatively, ascidians may prefer the patches with declining barnacles, or there could be an unknown external process that negatively affects barnacles and favors ascidians.

1. Introduction

The distribution of species in marine and terrestrial communities often forms a mosaic of patches at different stages of succession (Watt, 1947; Menge et al., 2005). Patch dynamics may be driven by recruitment and competition between several functionally similar taxa [e.g. grasslands (Tilman, 1997), marine hard bottoms (Keough, 1984)]. However, patches may also be created or modified by foundation species [sensu Dayton (1972), hereafter FS] that create habitats for many other taxa. Population structure and dynamics of FS can influence the spatial structure and dynamics of the whole assemblage, as has been found in mussel beds (Tsuchiya and Nishihira, 1986), seagrass meadows (Bruno and Kennedy, 2000), and aggregations of tube-building worms (Zühlke, 2001). The structure of these assemblages is hierarchical, with the FS on the top and with numerous dependent species (Bruno et al., 2003).

Intraspecific competition affects the performance of sessile benthic FS and the structure of their small-scale aggregations [see Dayton (1985), Pullen and LaBarbera (1991), Rose and Dawes (1999), Stewart et al. (2007) for examples from kelp forests, barnacle clusters, seagrass beds and macroalgal clumps, respectively]. Multiple FS often coexist, as in mixed forest stands (Veblen et al., 1979) and mixed kelp forests (Dayton, 1985). However, interactions between multiple FS have been examined mostly in transition zones between the areas in which they are dominant (Witman, 1987; Bertness et al., 2006). FS dynamics in small-scale patches have been ignored, despite the potential for strong effects on dependent assemblages at these spatial scales.

Small epibenthic patches dominated by barnacles *Balanus crenatus* Brugiere and several species of solitary ascidians [*Styela* spp., *Molgula* spp. and *Boltenia echinata* (L.)] are common on shallow subtidal soft-bottoms of the White Sea. These multi-tier clusters develop on empty bivalve shells and stones scattered on the muddy bottom. Primary substrates, such as empty shells of the clam *Serripes groenlandicus* (Brugiere) and small stones (Yakovis et al., 2004), are usually covered by living barnacles and their empty shells (hereafter “dead barnacles”). Dead barnacles degrade slowly and often remain attached to the substrate. At the study site ascidian clumps occur on barnacles live and dead, but almost never on primary substrate (Yakovis et al., 2008). The

* Corresponding author. 105-23, pr. Veteranov, 198261, St.-Petersburg, Russia. Tel.: +7 921 9874907; fax: +7 812 4507870.
E-mail addresses: marina.nikolaeva@gmail.com (M. Varfolomeeva), a.artemieva@gmail.com (A. Artemieva), n_shunatova@yahoo.com (N. Shunatova), yakovis@rbcmail.ru, e.yakovis@gmail.com (E. Yakovis).

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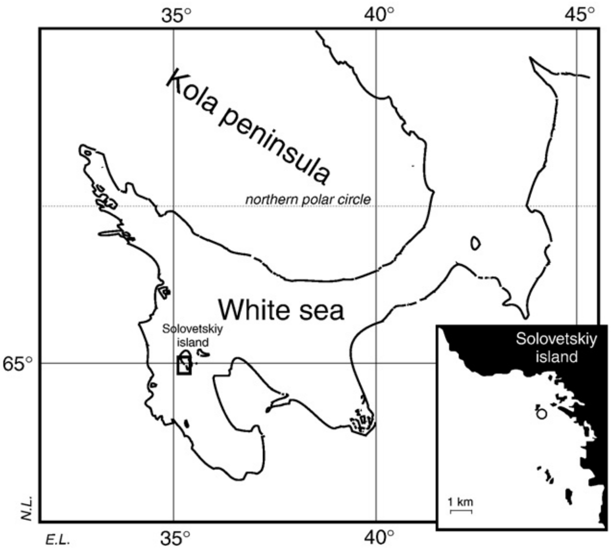

Fig. 1. Sampling site location (encircled).

clusters with various proportions of barnacles and ascidians co-occur at the same site. The diverse dependent assemblage includes various sessile (bryozoans, hydroids, red algae) and mobile (polychaetes, amphipods, gastropods and bivalves) organisms (Yakovis et al., 2004, 2005, 2007).

Empty substrates are initially colonized by barnacles, and ascidians are rarely found there (Yakovis et al., 2005). Most small barnacles are found on the primary substrate and conspecifics. Ascidians recruit to the surfaces of barnacle shells and conspecifics. The proportion of dead barnacles in a given size-class is greater in ascidian-dominated patches. One of the possible processes underlying this pattern is competitive exclusion of barnacles by ascidians (Yakovis et al., 2008). Ascidians also often grow inside the orifice and on the mobile plates of barnacle shells and thus may directly kill barnacles (Yakovis et al., 2008). Alternatively, ascidians may prefer the patches with declining barnacles, or there could be an unknown external process that negatively affects barnacles and favors ascidians.

Growth in barnacles often decreases in case of competition and thus is widely used to assess its intensity (Bertness, 1989; Bertness et al., 1999; Leonard, 2000; Lohse, 2002). Barnacles living in arctic and sub-arctic conditions develop annual rings of growth cessation on the outer shell surface (Bourget, 1980). We used vertical growth reconstructed from annual growth marks on the shell surface and dead:live ratios as a measure of the fitness of barnacles.

Unlike bivalves and polychaetes, ascidians are firmly attached to their substrates and we could not manipulate their density or presence by their exclusion (which destroys small patches) or by addition (because the manipulations attract crabs and other predators). Consequently, we regard the field observations on growth increments as the necessary first step to assess the potential negative effect of ascidians on barnacles. In present study we examined how the recent growth and dead:live ratios in the corresponding age classes of barnacles *Balanus crenatus* differ between the neighboring natural barnacle- and ascidian-dominated patches. The absence of the detectable correlation between the ascidian dominance and growth and survival of barnacles would suggest no effect of ascidians on barnacles (i.e., no competitive exclusion); the presence of the correlation, however, would require further experiments for evident conclusions.

2. Methods

2.1. Study site

Substrates with ascidians and barnacles were collected 100 m to the SW off the Solovetsky island (Onega Bay, White sea) (65°01.2′ N, 35°39.7′ E, Fig. 1). Sea bottom landscapes are variable near the Solovetsky archipelago with hard and mixed sediments predominating. The study site has a muddy bottom at a depth of 11–15 m. The bottom water temperature in July is 8 °C, and salinity varies between 24.4 and 27.6‰ (see Yakovis et al., 2005 and references therein).

2.2. Sampling and laboratory techniques

In July 2004 and 2005 SCUBA divers collected relatively large clusters of barnacles and ascidians (50 in total, with 1933 barnacles and 779 ascidians). The divers chose the clusters where the domination of either barnacle or ascidians was visually detectable. Later the patches were assigned either to ascidian-dominated (A) or barnacle-dominated (B) type based on the ratio of ascidian to barnacle biomass (A if greater or equal then 1, B if less then 1). Two areas separated by 30 m were sampled in 2004 (15 and 20 patches) and one in 2005 (15 patches) due to logistical constraints.

To identify the age of live and dead *Balanus crenatus* we counted the growth rings on each of the immobile undamaged shell plates. When growth rings were inconsistent among the plates, the number observed on the majority of plates was used. Growth increments (hereafter GI) were measured along the median of each plate and the length of the corresponding GIs averaged across the plates was used to quantify the individual growth.

To check the correspondence between the number of growth rings and the actual age, we reared barnacles in the field on initially clear clam shells and concrete blocks for 8 years 1998–2006 (see Yakovis et al., 2005). In July 1998–2002 at the site shown on Fig. 1 we added uncolonized dead shells of *Serripes groenlandicus* so that in 2004–2006 we could collect 2795 individuals of *Balanus crenatus* from 40 substrates with an exposure term (hereafter the time over which added substrates were available for recruitment) of 4–8 years. The age distribution of barnacles obtained from the analysis of growth rings then was matched to exposure term to check for consistency. The growth rings counted on the oldest individuals exactly matched the exposure term of substrates except for exposure term of 5 years, where barnacles with only 4 or less growth rings were found (Table 1). Given the single exception, we considered that the accuracy of age estimation from growth rings was sufficient for use in further analyses.

We determined the total wet weight of live barnacles and ascidians to the nearest milligram in each patch. Before weighing ascidians were pierced through branchial cavity and dried with filter paper to remove excess water. The biomass of conspecific neighbors was determined for each barnacle. We considered any pair of individuals as neighbors if the bases of their shells fused or if one of them grew on the other's shell surface.

Table 1
Distribution of the number of growth rings on the shells of barnacles *Balanus crenatus* reared in the field on initially uncolonized shells of *Serripes groenlandicus* with different exposure term

Number of growth rings	Exposure term, years				
	4	5	6	7	8
N.a.	1	2	3	0	4
0	186	284	129	129	237
1	21	92	55	159	3
2	23	105	18	12	5
3	181	468	14	6	6
4	5	71	50	9	5
5			59	32	11
6			248	50	26
7				45	21
8					20
Total	417	1022	576	442	338

N.a.-growth ring count is not available.